

MODE OF LIFE OF A GIANT CAPULID GASTROPOD FROM THE UPPER CRETACEOUS OF SAGHALIEN AND JAPAN

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ABSTRACT. The life habits of a huge Campanian patelliform gastropod, hitherto called '*Helcion giganteus*', from Saghalien and Japan are discussed on the basis of several specimens adhering to enormous shells of *Inoceramus* (*Sphenoceramus*) *schmidt*i. This gastropod is here transferred to the Capulidae of Mesogastropoda, and a new generic name, *Gigantocapulus*, is proposed for it. Its ecological relation with *I. (S.) schmidt*i is regarded as parasitic by analogy to some living species of *Capulus* that attach to the valves of pectinids. This interpretation is supported by stratigraphic and geographic distribution patterns and by its functional morphology.

'*Helcion giganteus*', originally described by Schmidt (1873) from the Upper Cretaceous at Cape Dui near Alexandrovsk, north Saghalien, is probably the largest patelliform gastropod known. Its shell sometimes exceeds 400 mm in maximum length, and shows a wide range of morphological variation. This species, though restricted to the lower to middle Campanian (Zone of *Inoceramus schmidt*i), occurs at various localities in Saghalien, Japan (mainly Hokkaido), Koryak Highland of eastern Siberia (Dundo and Efremova 1974), Southern Alaska (Jones, pers. comm.), and British Columbia (Whiteaves 1903). The association of this species with *I. (Sphenoceramus) schmidt*i Michael, 1899, is important. Almost all the specimens of '*I. digitatus*' described by Schmidt (1873) together with '*H. giganteus*' from Cape Dui seem to be referable to *I. (S.) schmidt*i, as revised in Michael (1899) and Nagao and Matumoto (1940). Their coexistence in the same fossil bed (commonly fine-grained sandstone) was also recorded at many other localities: Naibuchi (= Naibuti) (Matumoto 1942, p. 167) in south Saghalien, Abeshinai (Matumoto 1942, p. 205), Hetonai (Matumoto 1942, p. 251), Urakawa (Matumoto 1942, p. 268; Kanie 1966, p. 322; 1977, p. 54) and some other places in Hokkaido, and Dogo-Himezuka, Matsuyama City (Kashima 1972; Matsumoto 1973) in Shikoku.

Summarizing the classification and evolutionary history of Cretaceous patelliform gastropods in the northern Pacific region, Kanie (1975) concluded that '*H. giganteus*' belongs to the Mesogastropoda and that they possibly attached to some other shelled organism. Since '*H. giganteus*' is seldom accompanied by molluscs assumed to have lived on near-shore rocky substrates, it was assumed that it may have been attached to large bivalves such as *I. (S.) schmidt*i, but at that time there was no direct evidence. Subsequently Hayami found a specimen of '*H. giganteus*', in growth position attached to the shell surface of *Inoceramus*, in the collection of the University Museum, University of Tokyo. We have now examined the relation between the two molluscs on the basis of many specimens stored at various institutions. In the present article we describe some of these specimens, discuss the interpreted life habit of this gastropod, and compare it with some living species of similar habit. The taxonomic position of '*H. giganteus*' is also reconsidered.

SYSTEMATIC PALAEOLOGY

Order CAENOGASTROPODA Cox, 1959

Suborder MESOGASTROPODA Thiele, 1925

Superfamily CALYPTRAEACEA Lamarck, 1809

Family CAPULIDAE Fleming, 1822

Genus *Gigantocapulus* Hayami and Kanie, gen. nov.

Type species. *Helcion giganteus* Schmidt, 1873, northern Pacific region, Campanian.

Diagnosis. Shell very large, cap-shaped or conical, bilaterally symmetrical but more or less irregular in outline; apex located anteriorly from the centre, sometimes marginal; surface commonly ornamented with irregularly disposed radial costae in addition to concentric rings on the apical region; anterior elevated sector and internal septum absent; outermost layer prismatic, while other and inner layers are crossed-lamellar; some species living upon the shells of *Inoceramus*.

Remarks. The taxonomic position of '*H. giganteus*' and its allied species from the Cretaceous of northern Pacific has been debatable; *Capulus*, *Patella*, *Scurria*, *Acmaea*, and *Brunonia* also have been used as their generic names. Living patelliform gastropods occur in various unrelated taxonomic groups, e.g. the Patellacea of Archaeogastropoda, the Neritacea and Calyptraeacea of Mesogastropoda and the Siphonariacea of Pulmonata. Because their shell forms sometimes show remarkable convergence, such essential characters as muscle impression, presence or absence of internal septum and shell structure as well as inferable life habit may be important for determination of the taxonomic position of fossil species.

Kanie (1975) assigned these Cretaceous species in question to the genus *Anisomyon* Meek and Hayden, 1860, which had been included in the Basommatophora (an order of Pulmonata), and proposed a new family Anisomyonidae in the Mesogastropoda. This treatment was primarily based on the resemblance of muscle impressions and shell form of some species to the Capulidae and the difference of shell structure from the Siphonariidae. As noted elsewhere (Hayami and Kase 1977, p. 55), however, one of us (I. H.) doubted if the type species of *Anisomyon* [*H. patelliformis* Meek and Hayden, 1860] should be transferred from the Basommatophora to the Mesogastropoda, and presumed that '*H. giganteus*' may represent an unnamed genus of the Capulidae. This is proposed here, which modifies the previous classification (Kanie 1975) of Cretaceous patelliform gastropods from the northern Pacific region.

Kanie (1975) distinguished two 'morphotypes' in '*H. giganteus*': type A is characterized by the relatively small size, small apical angle, and irregularly noded ornament, while type B has relatively large size, large apical angle, and almost persistent and not noded radial ribs. Of the originally figured specimens of *H. giganteus*, most individuals including the lectotype (Schmidt 1873, pl. 2, fig. 17, designated by Kanie (1975) as 'holotype') belong to type B, and only two small specimens (Schmidt 1873, pl. 3, figs. 8, 9) may belong to type A. Numerous individuals of type A are preserved in various Japanese institutions, but none of them actually shows any intimate relation to the shell of *Inoceramus*. All the observed specimens attached to the surface of *I. (S.) schmidtii* belong to type B. Moreover, significant morphological differences are newly recognized between the two 'morphotypes'. First, a trace of an internal septum is often seen in type A (see Kanie 1975, p. 9, fig. 2), but has never been observed in type B. Secondly, the apex is always located subcentrally or even posteriorly in type A, while it is commonly located very anteriorly or even near the anterior margin in type B. Thirdly, a tongue-like projection, as described later, occurs only in type B. Host-determined non-genetic variation is actually known in a living capulid species (Thorson 1965), and dwarf males are also seen in such semi-parasitic gastropods. Yet, such great differences of essential characters are hardly explicable by individual variation. At present, we consider that the two 'morphotypes' belong to different species, and that the use of the specific name *Gigantocapulus giganteus* should be restricted to the type B of Kanie (1975). The specimens of type A seem to be close to '*A. transformis*' Dundo and Efremova (1974) from the Koryak Highland. The presence of an internal septum may suggest that they belong to the Calyptraeidae.

EXPLANATION OF PLATE 87

Figs. 1, 2. *Gigantocapulus giganteus* (Schmidt, 1873). UMUT MM5535 attached to the surface of *Inoceramus* (*Sphenoceramus*) *schmidtii* Michael, 1899. Loc. N469, north-west of Miho (gorge of Ryugase), Naibuchi area, south Saghalien. Collected by T. Matsumoto. 1, upper view, $\times 0.42$; 2, left lateral view, $\times 0.42$. (See also text-fig. 1.)



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HAYAMI and KANIE, Cretaceous patelliform gastropod

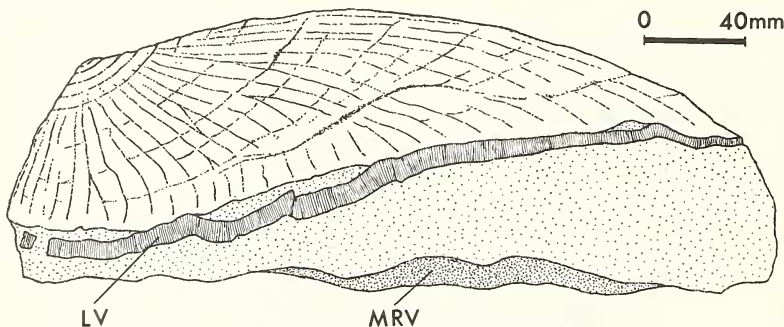
In the Western Interior of the United States some specimens of *Anisomyon* have also been found adhering to the shells of *Inoceramus* (Sohl 1967a). The association may be comparable with the present case. According to Sohl's (1967b) redescription of *A. patelliformis* (Meek and Hayden, 1856), however, one of the paratypes reveals clearly asymmetric muscle impression, which resembles that of *Siphonaria*, although the posterior carination of *Siphonaria*-type is undeveloped in that species. No specimen of *G. giganteus* shows clear muscle impression, but *Capulus*-like horseshoe-shaped muscle scars are recognized in *C. cassidarius* Yokoyama, 1890, which is considered to be ancestral to *G. giganteus* (Kanie 1975, p. 9, fig. 2). The genus *Anisomyon* is represented by much smaller species without radial costae, and we are now inclined to consider that it is not directly related to *Gigantocapulus*.

The genus *Brunonia* Müller, 1898, may be another Late Cretaceous patelliform gastropod comparable with our new genus from morphological and paleoecological standpoints. The genus was generally referred to the Siphonariidae, but in the *Treatise* (Knight *et al.* 1960) it was doubtfully included in the suborder Patellina. The concentrically ornamented shell of its type species [*B. grandis* Müller, 1898, from the Santonian of Germany] resembles the apical part of *G. giganteus*. Unfortunately, Müller's original specimen of *B. grandis* is said to have been lost, and further comparative study is now difficult. At present we think that *Gigantocapulus* is at least generically separable from *Brunonia* by the developed radial costae on the surface. Judging from the original figures of *B. grandis*, the apex is more constantly located near the centre of shell, and no projection is developed on its anterior periphery.

DESCRIPTION OF SELECTED SPECIMENS

Among a large number of specimens of *G. giganteus* in the collection of the University Museum, University of Tokyo (UMUT), and the Institute of Geology and Palaeontology, Tohoku University, Sendai (IGPS), several show an intimate association with the shells of *I. (S.) schmidtii*. UMUT MM5535 (Pl. 87; text-fig. 1) has well-preserved shells of the two species, and shows the position and orientation of attachment. It was found in T. Matsumoto's collection from a greenish fine-grained sandstone of the Ray 1 Member of the Ryugase Group at loc. N469 (gorge of Ryugase), about 4.5 km north-west of Miho, Naibuchi area, south Saghalien (see the locality map in Matsumoto 1942). The following description is entirely based on this specimen.

The shell of *G. giganteus*, though a considerable part of the marginal area is broken off, exceeds 290 mm in maximum length and 250 mm in breadth, showing a suboval, nearly bilaterally symmetrical, cap-shaped outline with a somewhat irregularly undulating marginal area. The apex is located at about one-fifth of maximum length

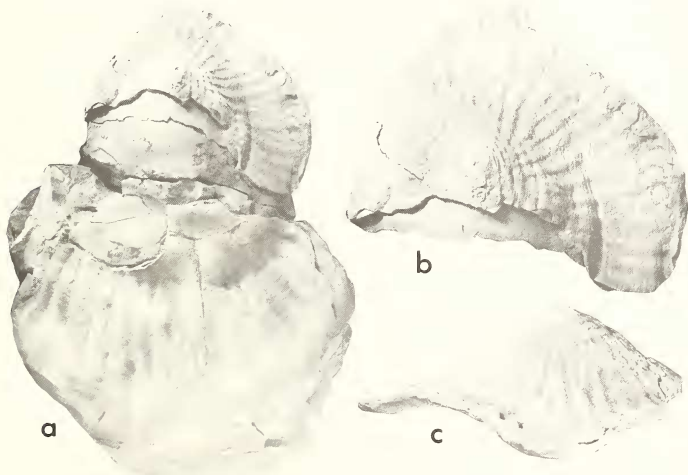


TEXT-FIG. 1. Sketch of Specimen I (UMUT MM5535) of *Gigantocapulus giganteus* (Schmidt) from the left side. LV: Fracture of the left valve (prismatic outer layer) of *Inoceramus (Sphenoceramus) schmidtii* Michael; MRV: Internal surface of the right valve of the same individual, on which characteristic divergent ribs are impressed.

from the anterior end, but the growth-lines indicate that it was situated near the centre of shell in the early growth stage. The pre-apical area steeply descends towards the anterior margin, while the post-apical area is widely expanded and broadly convex. The maximum inflation of shell lies far behind the apex. The surface is ornamented with several subconcentric ribs and about fifty radial costae. Subconcentric ribs are distinct and widely spaced, and their distribution is confined to the apical area (within 50 mm from the apex). On the contrary, radial costae are at first indistinct but become prominent after the effacement of subconcentric ribs. They are commonly irregularly dichotomous but sometimes convergent. The thickness of test does not exceed 10 mm. The outermost layer is thin and prismatic, and the outer and inner layers are crossed-lamellar and solid.

The associated shell of *Inoceramus* is evidently a part of an articulated individual. The shell of *G. giganteus* adheres closely to the surface of its left valve. The shell margin of *G. giganteus*, though its right side is incomplete, fits perfectly the undulating surface of *Inoceramus* without any perceptible gap (text-fig. 1). The opposite valve of *Inoceramus* has been almost entirely exfoliated and lost, but the divergent ribs impressed on the internal surface are unmistakably characteristic of *I. (S.) schmidtii*. The radial ribs of *G. giganteus* are evidently denser than the divergent ribs of *I. (S.) schmidtii*; the former does not necessarily correspond with the latter. Judging from the orientation of the divergent ribs as well as the nearly closed valves of *I. (S.) schmidtii* below the anterior margin of *G. giganteus*, this gastropod appears to have sat on the antero-ventral area of the living shell of *I. (S.) schmidtii* with the apex located on the antero-ventral side. The axis of symmetry of *G. giganteus* forms an angle of about 30° with the line of maximum length of *I. (S.) schmidtii*. The prismatic layer of *Inoceramus*, which represents the outer layer of the shell, is about 7.0 mm and 3.0 mm thick below the anterior and posterior margins of *G. giganteus*, respectively. The original size of this inoceramid shell would exceed 500 mm, provided that the thickness of this layer increases isometrically to the attained shell length. If the allometric growth indices calculated by Tanabe (1973, p. 177) on some specimens of *I. (S.) schmidtii* from Hokkaido are applied, the restored shell of this individual may exceed 700 mm in maximum length.

UMUT MM5711 (= Cr.1217) (text-fig. 2) is interesting because its right-anterior margin is nearly complete. It belongs to an old collection from the Cape Khoi Beds at Cape Jonquière near Alexandrovsk, north Saghalien.



TEXT-FIG. 2. *Gigantocapulus giganteus* (Schmidt). Specimen II (UMUT MM5711) attached to a crushed shell of *Inoceramus* (*Sphenoceramus*) *schmidtii* Michael. Loc. Cape Jonquière near Alexandrovsk, north Saghalien. *a*, upper view, $\times 0.36$; *b*, bird's-eye anterior view of the anterior part of the specimen showing a tongue-like projection and nearly complete right-anterior margin of shell, $\times 0.55$; *c*, anterior view of the same specimen, $\times 0.55$.

This individual is also closely associated with an enormous articulated shell of *I. (S.) schmidtii*, which, however, is so strongly crushed that the original state of attachment is difficult to restore.

This specimen is about 250 mm long and 190 mm wide, and the shell of post-apical part has been considerably exfoliated and lost. The matrix was successfully removed from the pre-apical part of shell, and both the external and internal characters are well exhibited. The marginal area of the pre-apical part is remarkably depressed and gently folded like a brim (text-fig. 2c). Furthermore, there is a curious tongue-like projection at the anterior extremity, which is unusually thickened with a rounded edge. The internal surface is nearly smooth, and neither a septum nor a muscle scar is observed below the apical area. Radial costae are not impressed on the internal surface even near the margin.

The following specimens of *G. giganteus* are also intimately associated with some crushed shells of *I. (S.) schmidtii*: UMUT MM5710 (= Cr.1418) and UMUT MM5709 (= Cr.998): old collection from the Zone of *I. schmidtii* in Naibuchi area, south Saghalien (exact locality unknown). UMUT MM5713 (= Cr.1228): old collection from the same locality as UMUT MM5711. UMUT MM5712 (= Cr.1218): old collection from the Zone of *I. schmidtii* in Alexandrovsk area, north Saghalien (exact locality unknown). These specimens show a wide range of morphological variation. One of the illustrated paralectotypes of *Helcion giganteus* from the type locality (Schmidt 1873, pl. 3, fig. 2) may be another example of an attached specimen, because a fragmentary prismatic shell was indicated below it.

VARIABILITY OF SOME MORPHOLOGICAL CHARACTERS

When *H. giganteus* was originally described by Schmidt (1873), four varieties were distinguished by the different position of the apex. All the original specimens are included either in var. *a. depressa*, var. *β nasuta*, var. *γ retracta* or var. *δ centralis*. Kanie (1975, p. 23) designated a specimen of var. *depressa* as the 'holotype' of *H. giganteus*, but (Hayami and Kase 1977, p. 56) this procedure can be regarded as constituting valid lectotype designation. Dundo and Efremova (1974) regarded some of these varieties as distinct species, and referred *centralis* and *nasutus* to *Patella* and *Helcion*, respectively. However (Kanie 1975; Hayami and Kase 1977), none of these varieties (except for two small specimens of var. *depressa* (Schmidt 1873, pl. 3, figs. 8, 9) seems to constitute a distinct taxon, because the difference of apical position as well as other characteristics appears to be gradational within a single fossil population. The growth-lines of the present specimens show that the variability of apical position is partly due to ontogenetic transformation: the apex evidently shifts from the central part to the anterior portion of shell with growth. There is also a change of the direction of apex in the young stage. As shown in UMUT MM 5709 and some other small specimens, the very apex, if preserved, seems to point in the direction opposite to the expansion of shell. Although the apex is generally located posteriorly in many living species of *Capulus* and related genera, this ontogenetic change is one of the main reasons why we suspect here, unlike a previous interpretation (Kanie 1975), that the shorter end is actually anterior.

The shell form and surface ornamentation are also quite variable. Among the forty specimens we have observed at various institutions in Japan, the angle of ultimate apex in lateral view varies from 120° to 145°. The number of radial costae ranges from thirty-five to sixty-five. The thickened tongue-like projection at the anterior end of shell is also observable in some other specimens, e.g. one of the paralectotypes (Schmidt 1873, pl. 3, fig. 10) and IGPS no. 50910 (Kanie 1975, pl. 15, fig. 1a, b; Kanie 1977, pl. 2, fig. 4). It may be a widespread character in this species, but, as shown by the growth-lines on UMUT MM5535, 5711, its development is seen only in the later ontogenetic stage.

The range of morphological variation of *G. giganteus* is thus unusually wide. Such a great variability is unknown in any living species of the Patellacea, but comparable with that of some species of the Capulidae. The variable shell form and ornamentation of this species were probably influenced by the nature of the surface of the host.

INTERPRETATION OF MODE OF LIFE

From our observation on *in situ* specimens, it is likely that at least some individuals of *G. giganteus* grew on living shells of *Inoceramus (Sphenoceramus) schmidtii*. This is supported by the fact that the associated inoceramid shells are, even if crushed, commonly articulated. Moreover, the stratigraphic

and geographic distribution of the two species is identical, which suggests not only their intimate ecological relation but also that the evolutionary history of the former depended on the latter.

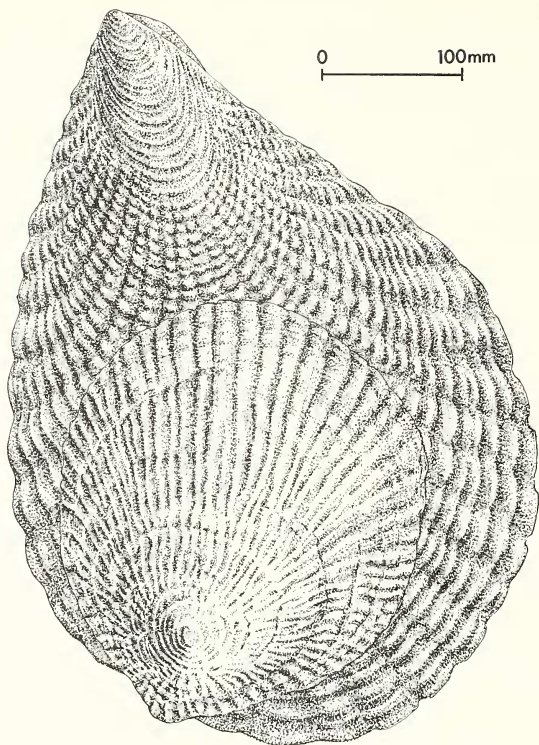
A large number of malacologists and marine ecologists have paid attention to the parasitic or semi-parasitic life of *Capulus* species and their hosts (Orton 1912, 1949; Yonge 1938; Otuka 1939; Teramachi 1942; Kuroda 1951; Sharman 1956; Burch and Burch 1961; Orr 1962; Thorson 1965; Kosuge and Hayashi 1967; Habe 1967). The hosts are commonly epifaunal bivalves, especially large species of the Pectinacea, though in a few cases the epibionts rest also on the surface of certain gastropods, brachiopods, and annelids. Sometimes an almost exclusive relation exists between the epibiont and host species (e.g. *C. tosaensis* on *Propeamussium sibogae* in Japan), but in other cases an epibiont species can grow on various hosts (e.g. *C. dilatatus* on *Amusium japonicum*, *Pecten albicans*, *Decatopecten striatus*, *Chlamys nobilis*, etc. in Japan; *C. ungaricus* on *P. maximus*, *Aequipecten opercularis*, *Modiolus modiolus*, *Monia patelliformis*, *Turritella communis*, etc. in Great Britain and North Sea). According to Yonge (1938) and others, *C. ungaricus* is a ciliary feeder. It intercepts the food, which has been collected on the gills of a bivalve, by inserting its long proboscis inside the bivalve shells. The ecological relation was regarded as semi-parasitic by Sharman (1956) and as commensalistic by Thorson (1965). Although the epibiont does not seem to cause the bivalves any mortal harm, this state is most certainly disadvantageous to the host. We consider that this is a case of external parasitism, but the term 'semi-parasitic' may be more appropriate for this species, because it also attaches to dead shells and rocks.

The life habits of such parasitic individuals of *Capulus* can be classified into two types. One is represented by *C. dilatatus*, in which (Kosuge and Hayashi 1967) the epibiont bores a small hole through the pectinid shell (commonly up-facing valve) in order to insert its proboscis. The boring position is concentrated on the anterior half of the disc (corresponding to the position of gills) and sometimes on the anterior wing. The orientation of attachment seems to be almost random. The other type is exemplified by *C. ungaricus*, which rests preferentially on the anterior and ventral marginal part of down-facing valves of living pectinids. Sharman (1956) examined the attaching position and orientation of many individuals of this species on the shells of *A. opercularis* from off the coast of the Isle of Man, noting: 'in its characteristic position the gastropod sits at the edge of the valve with the front margin of the shell projecting a little over it and the apex pointing inwards.' *C. ungaricus* never makes a borehole, but the edge of the valve margin is said to be frequently chipped so that this gastropod can easily insert its proboscis into the pectinid valves. Somewhat similar feeding habits are known in *C. tosaensis* from the Japanese deep waters, although this species is said to attach preferentially to the left (? up-facing) valve of *Propeamussium sibogae*.

On the shell surface of the many specimens of *I. (S.) schmidtii* neither a borehole nor a scar of attachment has been recognized, and it may be difficult to know whether the valve margin was actually chipped or not by other organisms. However, the attaching position and orientation in the specimens on text-fig. 1 seem to indicate that the life habit of *G. giganteus* was analogous to the second type, especially to the case of *C. ungaricus* as illustrated by Sharman (1956, figs. 1-3). We interpret the function of the curious tongue-like anterior projection as protecting the head of the gastropod which presumably protruded a little beyond the edge of the valve margin, because otherwise the remarkable, declined margin of this projection could not adhere closely to the surface of inoceramid shell. Such a hanging front margin of the shell is also commonly seen in *C. ungaricus*. Text-fig. 3 shows a putative living position of *G. giganteus* on the left valve of *I. (S.) schmidtii*, although it is still unknown whether the valve is actually up-facing or down-facing.

SUMMARY

The observation of *in situ* specimens and the functional interpretation of the shell shows that *G. giganteus* was a parasitic gastropod to *I. (S.) schmidtii*. Considering the much smaller size of other associated molluscs, only this inoceramid seems to have offered the solid ground of attachment for such a large patelliform gastropod. Although complete specimens of *I. (S.) schmidtii* can seldom be



TEXT-FIG. 3. Reconstruction of the living position of *Gigantocapulus giganteus* (Schmidt) on *Inoceramus* (*Sphenoceramus*) *schmidtii* Michael. Their periostracum is not drawn, because nothing is known about its development. This is not a sketch but chiefly based on Specimens I and II.

obtained, we have actually observed several extraordinarily large specimens of this species (exceeding 700 mm in maximum length) in the collections from Saghalien and Hokkaido. The gigantism of this gastropod is evidently related to the unusually large size of the host. If such a parasitic relation was developed, it can be readily imagined that an ecologically specialized epibiont was compelled to become extinct by the decline of the host species. *G. giganteus* seems to have shared its evolutionary lot with *I. (S.) schmidtii*, because their stratigraphic and geographic distribution is identical.

The history of this external parasitism possibly goes back to earlier times. As interpreted previously (Kanie 1975), *G. giganteus* may have been derived from *C. cassidarius* Yokoyama through some intermediate form. *C. cassidarius* is common in the Turonian to Santonian strata of the same region and is frequently accompanied by *I. (S.) naumanni* Yokoyama, which seems to be ancestral to *I. (S.)*

schmidtii, and some other small-sized species of *Inoceramus*. Therefore, it is possible that the parasitism was already established between the ancestors, although *in situ* preservation has not been found. The inferred mode of life also explains shell orientation, the wide range of morphological variation, and the curious tongue-like anterior projection in *G. giganteus*. Its taxonomic reference to the Capulidae of Mesogastropoda is also consistent with the parasitic mode of life. There is still a shortage of *in situ* material showing life orientations, which will provide more evidence of the paleoecological relation between this peculiar limpet and other organisms.

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